Why does noise reduce response to alarm calls? Experimental assessment of masking, distraction and greater vigilance in wild birds

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Abstract

1. Environmental noise from anthropogenic and other sources affects many aspects of animal ecology and behaviour, including acoustic communication. Acoustic masking is often assumed in field studies to be the cause of compromised communication in noise, but other mechanisms could have similar effects.
2. We tested experimentally how background noise disrupted the response to conspecific alarm calls in wild superb fairy-wrens, *Malurus cyaneus*, assessing the effects of acoustic masking, distraction and changes in vigilance. We first examined the birds' response to alarm-call playbacks accompanied by different amplitudes of background noise that overlapped the calls in acoustic frequency. We then scored and videoed their response to alarm calls in two types of background noise, that did or did not overlap call frequency, but were broadcast at a constant amplitude.
3. Birds were less likely to flee to alarm calls in higher amplitudes of overlapping noise, demonstrating that noise itself compromised communication independently of environmental correlates. Background noise affected the response only if it overlapped in frequency with the alarm calls, implying that the effect was not due to distraction. Further, birds were equally vigilant during background noise of overlapping or non-overlapping frequency, indicating that the lack of response to alarm calls in overlapping noise was not due to enhanced vigilance and awareness that there was no predator.
4. We conclude that alarm-call reception was compromised by masking, a mechanism that is often assumed but rarely tested in an ecological context. Masking compromised reception of high-frequency 'aerial' alarm calls and so could reduce survival in background noise of similar frequency. While anthropogenic noise, which is often of lower frequency, is unlikely to affect communication with these calls, it could affect

reception of acoustic cues of danger, or other conspecific or heterospecific alarm calls.

Keywords: alarm call, anthropogenic noise, anti-predator behaviour, birds, ambient noise, acoustic communication

1. Introduction

Environmental noise affects many aspects of animal behaviour, and is of conservation interest because of the growing global problem of anthropogenic noise. Anthropogenic noise from resource extraction, industry and transportation is now pervasive in both aquatic and terrestrial ecosystems around the world, and can disturb wildlife and affect the physiology, behaviour and fitness of species in diverse taxa (Barber, Crooks & Fristrup 2010; Slabbekoorn *et al.* 2010; Morley, Jones & Radford 2014; Shannon *et al.* 2015; Kunc, McLaughlin & Schmidt 2016; Cox *et al.* 2018). The most commonly studied behavioural impact of anthropogenic noise is that on acoustic communication, where the empirical focus has been on effects rather than mechanisms (Slabbekoorn & den Boer-Visser 2006; Chan *et al.* 2010; Francis & Barber 2013; Radford, Kerridge & Simpson 2014; Shannon *et al.* 2015; Morris-Drake *et al.* 2017; Cox et al. 2018). However, understanding mechanisms is important because it can help predict effects of noise and suggest methods to ameliorate these effects (Francis & Barber 2013). For example, remediation aimed at reducing acoustic masking may not solve problems of distraction or aversion (Luo et al. 2015; Senzaki et al. 2018). Here we focus on the mechanisms by which environmental noise can affect response to acoustic signals and thereby compromise communication.

Animals communicate acoustically for many reasons, and environmental noise—including anthropogenic noise—can affect both signaller and receiver behaviour. Animals produce a wide range of acoustic signals to communicate about, for instance, reproductive status, territory ownership, hunger, food and danger (Bradbury & Vehrencamp 2011). However, most studies investigating impacts of noise have considered bird song or other signals used to attract mates and defend space (Aubin & Jouventin 1998; Brumm 2004;

71 Brumm & Slabbekoorn 2005; Read, Jones & Radford 2014; Shannon *et al.* 2015). Signallers
72 may change their singing behaviour—for instance, the time of day that they vocalise and
73 acoustic characteristics of songs—as a consequence of noise, and receiver responses to song
74 can be compromised in noisy conditions (Slabbekoorn & den Boer-Visser 2006; Halfwerk *et*
75 *al.* 2011; Brumm & Zollinger 2013; Read, Jones & Radford 2014; Moseley *et al.* 2018). Far
76 less work has considered how noise affects other types of acoustic communication, including
77 anti-predator signalling (Lowry, Lill & Wong 2012; Potvin, Mulder & Parris 2014; Kern &
78 Radford 2016; Morris-Drake *et al.* 2017). Compromised response to signals about predators
79 is likely to reduce survival, so it is important to understand constraints imposed by noise
80 (Templeton et al. 2016).
81
82 Alarm calls are used to warn others of danger, but relatively little research has
83 examined the impact of noise on the response by listeners to these acoustic signals. Many
84 mammals and birds produce acoustic alarm signals in response to predators, using them to
85 warn others of imminent danger or to recruit assistance when mobbing threatening species
86 (Klump & Shalter 1984; Hollén & Radford 2009; Zuberbühler 2009). Conspecific receivers
87 benefit from being warned of danger (Caro 2005), and many animals also benefit by
88 eavesdropping on heterospecific alarm calls (Magrath *et al.* 2015a). The few experiments so
89 far show that additional noise can compromise both conspecific and heterospecific receiver
90 responses to alarm calls. For instance, nestling tree swallows (*Tachycineta bicolor*) crouched
91 and stopped calling in response to parental alarm calls during quiet conditions, but failed to
92 do so during playback of white noise (McIntyre, Leonard & Horn 2014). Similarly, great tits
93 (*Parus major*) usually approached a loudspeaker playing conspecific mobbing calls during
94 simultaneous playback of low-amplitude but not high-amplitude traffic noise (Templeton,
95 Zollinger & Brumm 2016). Responses to heterospecific alarm calls can be similarly

96 compromised: dwarf mongooses (*Helogale parvula*) were less likely to flee to tree squirrel
97 (*Paraxerus cepapi*) alarm calls during traffic-noise playback compared to ambient-sound
98 playback (Morris-Drake *et al.* 2017), and northern cardinals (*Cardinalis cardinalis*) failed to
99 respond to tufted titmice (*Baeolophus bicolor*) alarm calls in noisier locations near roads
100 (Grade & Sieving 2016).
101
102 Auditory masking is the most-commonly evoked mechanism to explain why noise
103 compromises communication. Masking occurs when there is an increase in the threshold for
104 detection or discrimination of an acoustic signal because of noise at similar acoustic
105 frequencies (Moore 2012). Laboratory studies find that the response to a test signal declines
106 monotonically with increasing amplitude of noise (partial masking), until there is no longer
107 any response (complete masking; Lohr, Wright & Dooling 2003; Brumm & Slabbekoorn
108 2005; Dooling & Blumenrath 2013). Partial masking implies that the signal is detectable but
109 the detail is hard to discriminate, while complete masking implies that there is no detection of
110 the signal (Clark *et al.* 2009; Kleist *et al.* 2016). Clearly, masking does occur in the
111 laboratory with the appropriate frequency and amplitude of noise, but the ecological question
112 is how masking or other mechanisms compromise communication in the wild. In general,
113 acoustic communication becomes more difficult as the amplitude of background sound
114 increases for birds, marine mammals, fish and amphibians, which is consistent with masking
115 (Fay & Megela-Simmons 1999; Brumm & Slabbekoorn 2005; Clark *et al.* 2009; Dooling,
116 West & Leek 2009), but does not exclude other mechanisms.
117
118 Whilst auditory masking is often assumed to be the primary mechanism by which noise
119 reduces the response to acoustic signals including alarm calls, other mechanisms, including
120 receiver distraction or changes in vigilance, could have similar effects on response (Brumm

121 & Slabbekoorn 2005; Francis & Barber 2013; Senzaki *et al.* 2018). Noise could distract
122 receivers and so compromise responses to other sensory input (Chan *et al.* 2010; Chan &
123 Blumstein 2011). For instance, road-noise playback disrupted the adaptive responses of dwarf
124 mongooses to predator faeces; since there was no auditory element to the predator cue, this
125 cross-modal effect of noise implies distraction (Morris-Drake, Kern & Radford 2016).
126 Similarly, fathead minnows (*Pimephales promelas*) subjected to motorboat noise failed to
127 respond to conspecific chemical alarm cues (Hasan *et al.* 2018), and crabs distracted by boat
128 noise responded with a greater delay to a silent looming object (Chan *et al.* 2010). However,
129 we know of no direct tests of whether acoustic distraction disrupts communication. Noise
130 might also affect communication if it prompts animals to increase vigilance, as is found, for
131 example, in chaffinches (*Fringilla coelebs*), house sparrows (*Passer domesticus*), California
132 ground squirrels (*Otospermophilus beecheyi*) and dwarf mongooses (Quinn *et al.* 2006;
133 Rabin, Coss & Owings 2006; Meillère, Brischoux & Angelier 2015; Kern & Radford 2016).
134 This increased vigilance could then affect the response to alarm calls, because an animal has
135 greater personal knowledge. Animals may therefore respond less to playback of alarm calls
136 because they know that there is no predator nearby (Morris-Drake *et al.* 2017). Overall,
137 discriminating the effects of masking, distraction and increased vigilance is difficult because
138 all three can predict a decline in responses to alarm calls in the presence of noise.
139
140 In this study, we investigate experimentally how and why background environmental
141 noise reduces the response of wild superb fairy-wrens (*Malurus cyaneus*) to conspecific
142 alarm calls. Fairy-wrens give aerial alarm calls to predatory birds in flight and, under quiet
143 conditions, almost always flee to cover after multi-element versions of these calls, which
144 signal immediate danger (Fallow & Magrath 2010). This conspicuous behaviour provides a
145 clear and sensitive assay of response to an acoustic signal when birds are challenged with

different amplitudes and types of noise. We therefore began with an experiment to quantify the reduction in response to aerial alarm calls under different amplitudes of background noise that overlapped calls in frequency. We then assessed in a second experiment why noise reduced the alarm-call response, broadcasting either overlapping or non-overlapping noise and quantifying vigilance. Together these experiments allowed us to test the potential mechanisms of masking, distraction and greater vigilance.

2. Materials and methods

(a) Study species and site

Superb fairy-wrens are small passerines (9–10 g) that forage primarily on the ground (Higgins, Peter & Steele 2001). They are territorial cooperative breeders that usually breed from September to January, although outside the breeding season they often join groups and move across adjacent territories (Rowley 1965). The sexes can be distinguished by plumage and bill colour after gaining adult colours (Higgins, Peter & Steele 2001). Fairy-wrens produce a variety of alarm calls, including aerial alarm calls to predatory birds in flight, mobbing calls to terrestrial and perched predators, distress calls when captured, and whining calls when mobbing cuckoos (Rowley & Russell 1997; Magrath, Pitcher & Gardner 2007; Colombelli-Négrel *et al.* 2010; Feeney *et al.* 2013). Their aerial alarm calls are composed of repeated elements, each about 100 ms long and with a mean peak frequency of about 9.1 kHz (Magrath, Pitcher & Gardner 2007). Fairy-wrens convey greater urgency of danger in their aerial alarm calls by including more elements; multi-element calls prompt immediate flight to cover, and birds remain in cover for longer when calls contain more elements (Fallow & Magrath 2010).

We studied an individually colour-banded population of fairy-wrens in the Australian National Botanic Gardens in Canberra (-35.279° S, 149.109° E). The population has been studied for over 30 years and the birds are accustomed to people (Cockburn *et al.* 2016). Fairy-wrens occur throughout most of the 40 ha Gardens, which contain natural woodland, areas planted with Australian native plants, and lawn. Collared sparrowhawks (*Accipiter cirrhocephalus*) and pied currawongs (*Strepera graculina*) are locally common predators of fairy-wrens (Magrath, Pitcher & Gardner 2009).

(b) Overview of experimental design

We used playback experiments on fairy-wrens to investigate the effect of background noise on the response to conspecific aerial alarm calls. In Experiment 1, we examined how different amplitudes of background noise affected the response to alarm calls. The background noise in this experiment overlapped in frequency with the alarm calls, so all potential mechanisms affecting response—masking, distraction and greater vigilance—were possible. In Experiment 2, we tested which of these potential mechanisms could explain the noise effect found in Experiment 1 (Results). To do so, we assessed how background noise playbacks with different frequencies but a constant amplitude affected responses to alarm calls and vigilance. Birds were never exposed to real predators, individuals that fled to playbacks returned to feed within 1 min, and we observed no adverse effects on birds.

193 (c) Sound-file preparation

194

195 Ambient sound recorded at the study site was used to prepare 16 unique background-noise
196 playbacks. We recorded 16 examples of ambient sound under relatively quiet conditions in
197 the Gardens, using a Sennheiser ME62 omnidirectional microphone and a Marantz PMD670
198 recorder sampling at 44.1 kHz and 16 bits. We then excised any distinct foreground sounds,
199 such as bird calls or nearby human noise, with remaining sections joined using the zero-
200 crossing function in Adobe Audition CS6, to produce background noise that was 20 s long.
201 This background noise was then filtered in Raven Pro 1.5 to produce two types of
202 background noise that differed in frequency range (**Figure 1**). 'Overlapping' noise ranged
203 from 6 to 10 kHz, which covers the range in peak frequency of fairy-wren aerial alarm calls
204 (8.6–9.5 kHz; Magrath, Pitcher & Gardner 2007). 'Non-overlapping' noise ranged from 2 to
205 6 kHz, so it had the same bandwidth as 'Overlapping' noise but did not overlap in frequency
206 with the alarms. This Non-overlapping frequency range is well within typical passerine
207 hearing (Dooling 2004), and fairy-wrens respond to heterospecific alarm calls that fall
208 completely within this range (Magrath, Pitcher & Gardner 2009; Magrath & Bennett 2012).
209 These 20 s noise tracks were faded in for 7 s and faded out for 5 s, to avoid abrupt changes in
210 amplitude that might startle birds. The middle 8 s of each background-noise track was of
211 relatively constant amplitude, with a standard deviation of average power over each second
212 of less than 0.5 dB. Finally, we adjusted the amplitude of background noise files to produce
213 the required target broadcast amplitude (below), as measured with a Brüel & Kjær 2240
214 sound level meter at 10 m. All calibrations and field playbacks used the same set of
215 equipment: a Roland Edirol R-05 HR digital recorder, connected to a custom amplifier and a
216 Peerless 810921 tweeter speaker (frequency response 2–11 kHz). Recordings of broadcast
217 noise showed that it was roughly flat within the given range. All the equipment was mounted

around the observer's waist as a mobile playback system, as used in previous experiments on fairy-wrens (e.g. Magrath *et al.* 2015b).

We prepared 16 playbacks of fairy-wren aerial alarm calls, each recorded from a different individual (**Figure 1**). Calls were prompted using gliding model pied currawongs or collared sparrowhawks (Magrath, Pitcher & Gardner 2007; Fallow & Magrath 2010), and recorded using a Sennheiser ME66 or ME67 directional microphone and Marantz PMD670 recorder sampling at 44.1 kHz and 16 bits. A single element was pasted at a natural interval to form four-element alarm calls (Fallow & Magrath 2010), which ranged from 0.43 to 0.97 s, depending on the duration of individual elements. We used four-element alarm calls because they indicate urgent danger and prompt immediate flight to cover (Fallow & Magrath 2010). Sound below 5 kHz was filtered out using Raven Pro 1.5. We broadcast alarm calls so that elements had a mean amplitude of 52 dB SPL at 10 m, which is similar to the mean natural amplitude at that distance (mean 56.5 dB at 4–7 m, implying 48.5 to 53.4 at 10 m; Magrath, Pitcher & Gardner 2007). Alarm-call amplitude was determined by re-recording playbacks at 10 m, along with a calibration tone that had its amplitude measured with the Brüel & Kjær 2240 level meter. The alarm-call files were then adjusted iteratively to achieve the target amplitude.

As described in detail below, experiments used playbacks of alarm calls alone, background noise alone, and alarm calls mixed with background noise. Each type of playback was broadcast from the single speaker; we used Adobe Audition CS6 to mix the calibrated alarm-call and noise files into mono files, such that alarm calls occurred during the period of stable, maximum noise amplitude. A single-speaker design has been used successfully in previous studies of the effects of noise on communication (e.g. Templeton, Zollinger &

243 Brumm 2016), allowed use of our mobile playback system, and ensured that the signal and
244 noise came from the same direction and distance, which prevented any spatial release of
245 masking or unwanted variation in distance. The time when the alarm call started in a specific
246 track (at 10, 11 or 12 s) was generated randomly by Excel, to reduce the possibility that birds
247 would habituate to a predictable temporal pattern.
248
249 (d) Field methods
250
251 Playbacks used a matched design, with all treatments broadcast at 16 locations spread across
252 the study site. As in several previous experiments on fairy-wrens (e.g. Magrath, Pitcher &
253 Gardner 2009; Magrath & Bennett 2012), we used a unique set of playbacks at each location,
254 and so used location as the unit of replication. We matched by location, rather than specific
255 individual, because in the non-breeding season individuals can wander over several
256 territories, and because location controls for ecological variables such as predator activity and
257 ambient sound. The matched design means any differences among locations will affect all
258 treatments equally. It is possible that individual differences add variance to the results, but
259 the randomised design ensures that this would not introduce bias. Playbacks at a given
260 location always entailed more than one individual in Experiment 1 (non-breeding season; 4–7
261 individuals per location), and did so in 12/16 locations in Experiment 2 (breeding season; 1–4
262 individuals per location). Of the 60 individuals in Experiment 1, 12 received playbacks at two
263 locations and one at three locations, but no bird received a specific treatment more than once.
264 All 33 individuals in Experiment 2 received playbacks at only one location, as the birds were
265 then territorial.
266

To ensure treatment order did not confound the response, such as through habituation, playback order was generated randomly in R at each location, but constrained over each experiment so that any one treatment was presented roughly evenly at each order. In Experiment 1, with seven treatments, this meant that each treatment almost always occurred 2 or 3 times at each order, and in Experiment 2, with five treatments, each treatment almost always occurred 3 or 4 times at each order. To reduce the risk of habituation to alarm calls, we broadcast at most two playbacks at each location on a given day, with at least 1 h between them. In practice, playbacks at a location were carried over a mean of 9.8 days (range 6–15) in Experiment 1 and 8.3 days (range 3–18) in Experiment 2, further reducing the risk of habituation. Response to the alarm-call playback was scored as fleeing to cover or not. We used the same score for playbacks to noise alone, taken from 10–12 s after the beginning of playback, so that it matched in time the playbacks that included alarm calls. All playbacks were carried out and scored by YZ, so there were no inter-observer issues to control.

Playbacks to wild individuals have the advantage of ecological validity, but the disadvantage that it is not possible to control fully the acoustic environment. We addressed this issue by using location as the unit of replication, restricting playbacks to relatively quiet periods and quantifying the ambient sound after every playback. We then calculated the contribution of ambient sound to the total amplitude experienced by the focal bird and found that it was negligible (Supporting Information).

(e) Experiment 1: effect of noise amplitude on the response to alarm-call playback

To investigate the effect of different amplitudes of noise on the response to aerial alarm calls, we broadcast alarm calls in combination with ‘Overlapping’ noise (6–10 kHz). Birds received

seven treatments: (1) aerial alarm call alone at 52 dB; aerial alarm call of 52 dB mixed with (2) 52 dB, (3) 55 dB, (4) 58 dB or (5) 61 dB Overlapping noise; and Overlapping noise alone at (6) 52 dB and (7) 61 dB. All dB levels refer to the amplitude at 10 m from the loudspeaker, which was similar to the distance to the focal bird during playbacks (mean 10.8 ± 1.0 SD, measured with a laser rangefinder). The aerial alarm call alone was the positive control, measuring response in the absence of experimental noise, and the two playbacks of noise alone tested whether the birds fled to the noise itself at the lowest and highest levels used in the experiment. Playbacks were done in the non-breeding season, between 12 May and 27 June 2017.

(f) Experiment 2: the mechanism of how noise disrupts alarm-call responses

To investigate the mechanism causing the reduced response to alarm calls in noise (Results, Experiment 1), we broadcast alarm calls mixed with noise with different frequency ranges, while simultaneously videoing the birds' responses. Birds received five playback treatments: (1) aerial alarm call alone (peak frequency c. 9.1 kHz) at 52 dB; (2) aerial alarm call at 52 dB mixed with 'Overlapping' noise (6–10 kHz) at 58 dB; (3) aerial alarm call at 52 dB mixed with 'Non-overlapping' noise (2–6 kHz) at 58 dB; (4) 'Overlapping' noise alone at 58 dB; and (5) 'Non-overlapping' noise alone at 58 dB. All amplitudes were measured at 10 m, which was similar to the mean playback distance of 11.2 m ± 1.0 SD, and again the aerial alarm call and noise-alone playbacks were controls. Background noise was set to 58 dB because this was the lowest amplitude at which birds no longer responded to alarm calls of 52 dB in Experiment 1 (Results). As well as scoring in the field whether the focal bird fled or not, we videoed birds with a Panasonic HC-V770M video camera (50 frames per s, resolution 1920*1080p) mounted on the observer's shoulder, and subsequently quantified the focal

bird's vigilance in the 10 s of noise immediately before the alarm playback in the mixed tracks. The videos were scored blind, frame-by-frame by YZ, after the names of video files were re-assigned by others and the sound was muted. Vigilance was scored as the proportion of frames when the bird had its head up, rather than oriented towards the ground (where fairy-wrens glean food). Head position is an indirect measure of the vigilance, but is a commonly used metric that correlates with exposure to greater risk in birds, such as being at the edge compared to centre of a flock (Beauchamp 2015). In at least in some species, a raised head position has been shown experimentally to increase the probability of detecting danger (e.g. Tisdale & Fernández-Juricic 2009). Playbacks were done in the breeding season, between 21 Nov 2017 and 1 Jan 2018.

The immediate response to playback and preceding vigilance allowed a test of the three mechanisms of how noise could affect the response to alarm calls. The flee response was used to discriminate acoustic masking from distraction. Acoustic masking predicts that birds will flee to alarm calls during Non-overlapping noise but not during Overlapping noise, while distraction implies a reduced response during either type of noise, compared to alarm calls alone, because both noise playbacks were of the same amplitude and lie well within avian hearing (Dooling 2004). A similar logic has been used to discriminate the effects of masking and distraction on the foraging performance of bats in the presence of noise (Luo, Siemers & Koselj 2015), and female frogs responding to male mating calls (Senzaki *et al.* 2018). A reduced response specifically during Overlapping noise could, however, also arise if birds were more vigilant during Overlapping noise, and so were aware that no predator was nearby and were therefore less likely to flee (Morris-Drake *et al.* 2017). We therefore quantified vigilance during the background noise immediately before the alarm playback to test if differences in vigilance could explain observed responses.

342

343 (g) Statistical analysis

344

345 Each experiment entailed repeated measures at 16 locations, so we used matched statistical
346 tests. Analysis of whether birds fled or not used Cochran Q tests for overall differences
347 among treatments and McNemar tests for paired comparisons, as both tests are designed for
348 matched, dichotomous data (Siegel & Castellan 1988). Vigilance was measured as a
349 continuous variable, so we used a paired t-test to compare vigilance during Overlapping and
350 Non-overlapping noise. We used the R statistical package (Team 2017), including the coin
351 package for Cochran Q and McNemar tests (Hothorn *et al.* 2008) and base package for t-
352 tests.

353

354 ## 3. Results

355

356 (a) Experiment 1: effect of noise amplitude on the response to alarm-call playback

357

358 None of the 16 fairy-wrens fled to cover during playbacks of Overlapping noise alone at
359 either the low or high amplitude extremes (**Figure 2**). This means that any fleeing by birds in
360 response to the mixed playbacks is due to the alarm calls and not noise.

361

362 Fairy-wrens were less likely to flee to cover to alarm calls as the amplitude of
363 Overlapping noise increased (**Figure 2**). Almost all birds fled to playback of alarm calls
364 alone, but this proportion was reduced with added noise, so that overall the response to alarm
365 calls was affected by noise (all five treatments with alarm calls: Cochran's Q test, $Q = 38.4$,
366 $df = 4$, $P < 0.001$). In addition, an increasing amplitude of noise in mixed treatments led to a

monotonic reduction in the response to alarm calls (four mixed treatments with alarm calls and noise playback: $Q = 21.6$, $df = 3$, $P < 0.001$). Birds no longer fled to alarm calls mixed with 58 dB or 61 dB noise, and pairwise comparisons revealed a significant drop in response from 55 to 58 dB (**Table 1=Figure 2**), consistent with a masking threshold between these values but potentially caused by any mechanism.

(b) Experiment 2: the mechanism of how noise disrupts alarm-call responses

The effect of noise on the response to alarm calls was consistent with acoustic masking rather than distraction (**Figure 3)**. While only 1 of 16 birds fled to cover in response to alarm calls mixed with Overlapping noise, all 16 birds fled in response to alarm calls mixed with Non-overlapping noise (McNemar test: Exact 2-tailed, $P = 0.004$). Consistent with the previous experiment, all birds fled to alarm calls alone and none fled to Overlapping noise alone. In addition, no birds fled to Non-overlapping noise alone.

There was no significant difference in our measure of vigilance that could account for the different response of birds to alarm calls mixed with Overlapping and Non-overlapping noise (**Figure 4)**. Birds were equally vigilant during Overlapping and Non-overlapping noise immediately before alarm calls (paired t-test, $t_{15} = 0.383$, $P = 0.96$).

4. Discussion

Background noise affected the response to alarm calls in wild fairy-wrens, probably only by acoustic masking rather than through distraction or changes in vigilance. In our first experiment, broadcasting background noise overlapping in frequency with alarm calls, birds

were less likely to flee to the alarm calls in higher amplitudes of noise. This shows that noise affected the response to alarm calls, but does not establish the mechanism. In our second experiment, background noise affected the response to alarm calls only if it overlapped in frequency with alarm calls, and not if it was non-overlapping. This implies that the reduced response was not due to distraction and was consistent with masking. Finally, birds showed the same level of vigilance in response to Overlapping and Non-overlapping noise, indicating that the lack of response to alarm calls mixed with Overlapping noise was not due to enhanced vigilance and awareness that there was no predator. Together our results indicate that alarm call reception was disrupted by acoustic masking, which is something that is likely to be common but, as far as we are aware, not previously shown in experiments on wild birds.

Experiment 1 showed that increased levels of background noise led to a reduced probability of fleeing to cover after aerial alarm calls. Almost all birds fled to alarms when not mixed with noise, but response declined monotonically until there was no response when mixed with noise at or above 58 dB. This experiment demonstrates that background noise itself affected the response to alarm calls, because playbacks were matched by location, eliminating potential confounds such as location-specific variation in predator density or effects of noisy infrastructure unrelated to noise itself (Grade & Sieving 2016; Antze & Koper 2018). Furthermore, birds did not flee to noise-only playbacks, showing that fleeing was to alarm calls and not the accompanying noise. Short-term playbacks of noise potentially provoke startle responses (Francis & Barber 2013), but we used locally recorded background sound that faded in over 7 s to a modest maximum amplitude, which may explain the lack of startling. Aerial alarm calls in fairy-wrens signal immediate threat from airborne predators (Magrath, Pitcher & Gardner 2007), so that any noise-induced reduction in response to these

417 alarm calls could prove fatal. More broadly, noise could affect the response to any acoustic
418 sources of information about danger, including conspecific and heterospecific alarm calls,
419 and acoustic cues from predators themselves (Magrath, Pitcher & Dalziell 2007; Corcoran,
420 Barber & Conner 2009; Barber, Crooks & Fristrup 2010; Haff & Magrath 2010).
421
422 The differences in immediate responses to alarm calls in Experiment 2 were consistent
423 with acoustic masking and unlikely to be due to distraction. First, masking occurs primarily
424 when noise is of a similar acoustic frequency to the signal (Brumm & Slabbekoorn 2005),
425 whereas distraction could occur regardless of the acoustic frequency of noise (Francis &
426 Barber 2013). Indeed, distraction can even be cross-modal, such as when noise affects the
427 perception of visual and olfactory stimuli (Chan *et al.* 2010; Chan & Blumstein 2011; Morris-
428 Drake, Kern & Radford 2016). Consistent with masking but not distraction, fairy-wrens
429 almost never fled to alarm calls when the experimental noise overlapped the frequency of
430 alarm calls, but always fled when the noise was of lower frequency, despite being the same
431 amplitude and well within passerine hearing (Dooling 2004). One caveat is that Overlapping
432 noise might be more distracting than Non-overlapping noise, but this seems unlikely since
433 birds showed no clear anti-predator response to either noise type alone and did not look up
434 more to Overlapping noise. Second, our results on wild birds replicate patterns of masking in
435 birds in the laboratory. Specific critical ratios for masking vary among species, frequencies,
436 and type of noise and signal (Dooling 2004), and so are difficult to compare, but our results
437 parallel laboratory studies, which show a monotonic decline in response with increasing
438 amplitude of overlapping white noise, eventually reaching a threshold beyond which there is
439 no response to the signal (Lohr, Wright & Dooling 2003; Dooling & Blumenrath 2013). By
440 contrast, the degree of distraction is not necessarily related in a simple way to amplitude, and
441 can be affected by the type of noise and the task being distracted (Smith 1989; Banbury *et al.*

2001; Naguib 2013). For example, speech and intermittent noise, but not regular white noise, commonly affect human performance on cognitive tasks; in our experiment both background noise types had similar features aside from a difference in frequency range.

Although the patterns of fleeing in Experiment 2 could in principle arise from increased vigilance during Overlapping noise, there was no evidence for this mechanism. Specifically, if playback of Overlapping noise prompted greater vigilance, then birds might not respond to the alarm calls because they already knew that there was no predator nearby, not because the calls were inaudible (Morris-Drake *et al.* 2017). Contrary to this explanation, blind-scoring of video revealed that there was no difference in the proportion of time birds had their head up during Overlapping and Non-overlapping noise immediately before the alarm call. The lack of a difference in our measure of vigilance is perhaps surprising, as noise that masks alarm signals might be expected make animals warier and so increase vigilance, and thereby enhance detection of predators or acoustic signals or cues of danger (Beauchamp 2015; Lynch *et al.* 2015). In support of these possibilities in other species, broadcast of traffic noise prompted black-tailed prairie dogs (*Cynomys ludovicanus*) to increase vigilance, which led to an earlier response during human approach (Shannon *et al.* 2014; Shannon *et al.* 2016); and California ground squirrels (*Spermophilus beecheyi*) were more vigilant when near noisy wind turbines, and in those locations also responded more strongly to audible alarm playbacks (Rabin, Coss & Owings 2006). However, in our study vigilance was unaffected by the acoustic frequency of noise, and therefore did not account for the pattern of fleeing to alarm calls, arguing against this alternative to masking.

Our study was designed to examine specifically the mechanisms by which noise reduced the response of fairy-wrens to their aerial alarm calls, but there are many

467 opportunities for research on how noise could affect alarm communication in this and other
468 species. First, masking alone appeared to be the critical mechanism reducing response to
469 alarm calls in our experiments, which means that low-frequency urban noise should not affect
470 reception of these high-frequency alarm calls. However, mobbing, distress and whining alarm
471 calls include lower frequencies (Colombelli-Négrel *et al.* 2010; Feeney *et al.* 2013) and so
472 could be partially masked by urban noise. Furthermore, low-frequency urban noise could
473 mask the sound of predators themselves, and so eliminate alternative information on danger
474 when high-frequency natural noises, such as cicada choruses, mask aerial alarm calls. The
475 effect of anthropogenic noise could therefore depend on the type of alarm call and concurrent
476 sources of noise. Second, we examined only the response to alarm calls, but it is also relevant
477 to consider alarm-call production (Brumm & Zollinger 2013). While there is limited
478 opportunity to increase the effectiveness of urgent alarm calls by adjusting the location or
479 timing of calling in noisier conditions, birds might modify alarm calls to make them more
480 audible. For example, callers can increase the amplitude of alarm calls (Templeton, Zollinger
481 & Brumm 2016), modify acoustic structure to increase their audible range (Potvin, Mulder &
482 Parris 2014), or beam calls to specific receivers (Yorzinski & Patricelli 2010). Nonetheless,
483 regardless of sender adaptations, receivers gain information from both conspecific and
484 heterospecific alarm calls from varying distances, so that noise rather than sensory acuity will
485 often limit the distance over which calls can be received (Klump 1996).
486
487 We conclude that masking, rather than distraction or changes in vigilance, accounted
488 for the noise-induced disruption of alarm communication in wild fairy-wrens. It would be
489 valuable to test explicitly for masking in other species, including of both alarm calls and
490 other cues of danger. More broadly, we advocate studies on how noise affects animal
491 behaviour, and suggest that multiple mechanisms, including distraction and vigilance effects,

will affect many species and are not be mutually exclusive (e.g. Luo, Siemers & Koselj 2015; Senzaki *et al.* 2018). Evaluating mechanisms is important in understanding the evolution of communication, predicting the effects of anthropogenic noise, and suggesting ways to ameliorate the consequences of this global pollutant (Francis & Barber 2013).

Author contributions

RDM and ANR conceived the study, all authors designed the study and contributed to writing, and YZ carried out fieldwork and analyses.

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Data accessibility

Data deposited in the Dryad Digital Repository: doi:10.5061/dryad.b4f2m1t, (Zhou *et al.* 2019).

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704 **Figure legends**

705

706 **Figure 1**. Sounds used during playback experiments: (a) aerial alarm call, (b) Overlapping
707 noise (6–10 kHz), and (c) Non-overlapping noise (2–6 kHz), each showing the waveform
708 (above) and spectrogram (below). Note the different time scale for the alarm call. Noise
709 playbacks were calibrated as needed in experiments, and some treatments entailed alarm calls
710 mixed with noise. Spectrograms were prepared in Raven Pro 1.5 and used a Blackman
711 window type, 5.8 ms window size and 95% overlap.

712

713 **Figure 2**. Proportion of fairy-wrens that fled to cover to Overlapping noise alone (Noise; 6–
714 10 kHz), alarm call alone (Alarm; mean peak frequency 9.1 kHz), and a 52 dB alarm call
715 mixed with different levels of Overlapping noise (+Noise). Probability values are from
716 McNemar tests of differences between adjacent columns, with increasing amplitude of
717 Overlapping noise. N = 16 locations for each treatment.

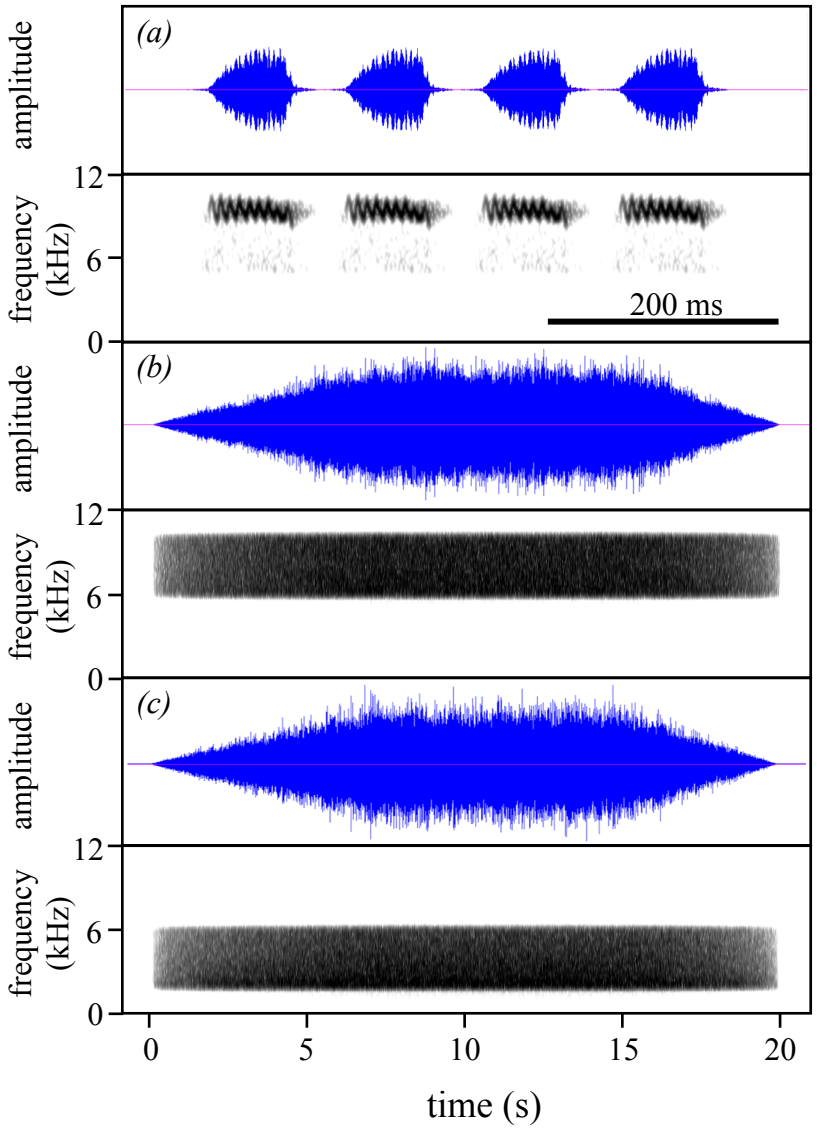
718

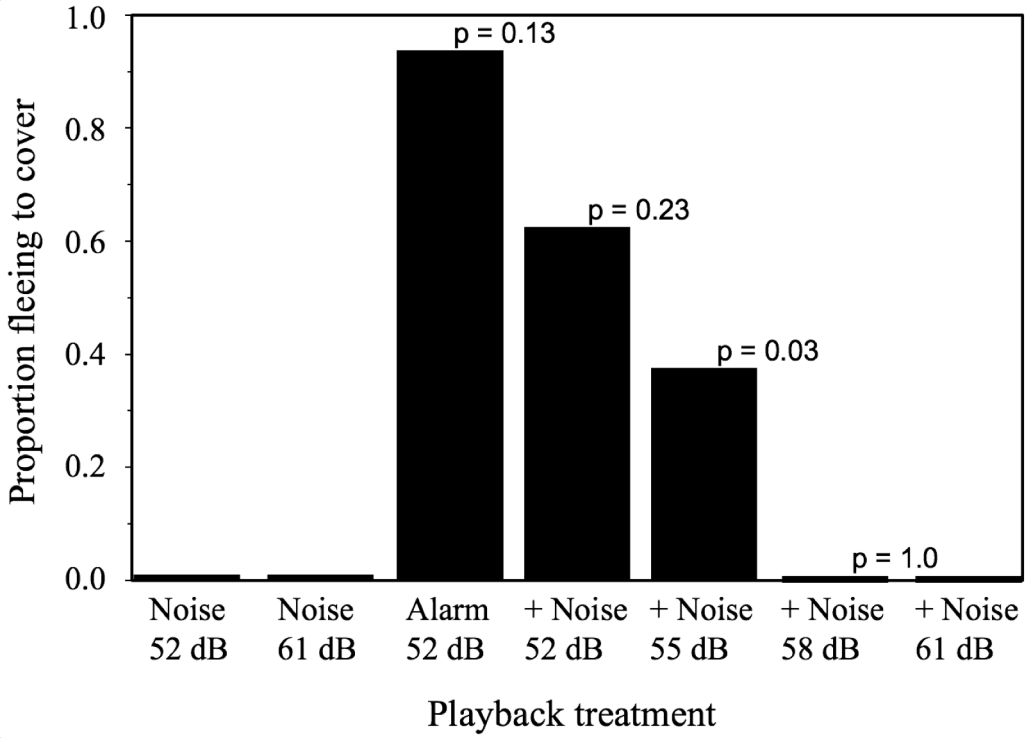
719 **Figure 3**. Proportion of fairy-wrens that fled to cover to Overlapping (6–10 kHz) and Non-
720 overlapping (2–6 kHz) noise alone, alarm call alone (mean peak frequency 9.1 kHz), and
721 alarm calls mixed with Overlapping or Non-overlapping noise. The probability value is from
722 a McNemar test for a difference in response to alarm calls mixed with Overlapping or Non-
723 overlapping noise. N = 16 locations for each treatment.

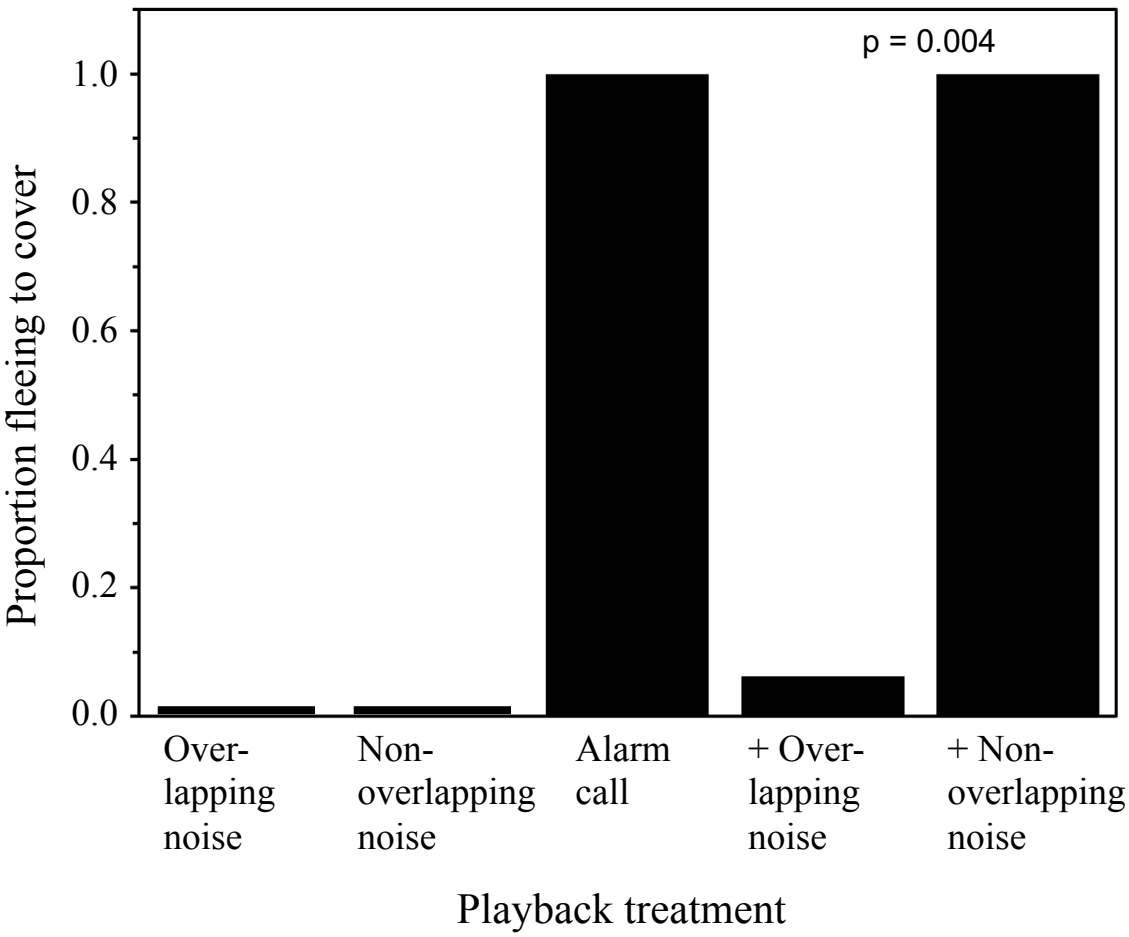
724

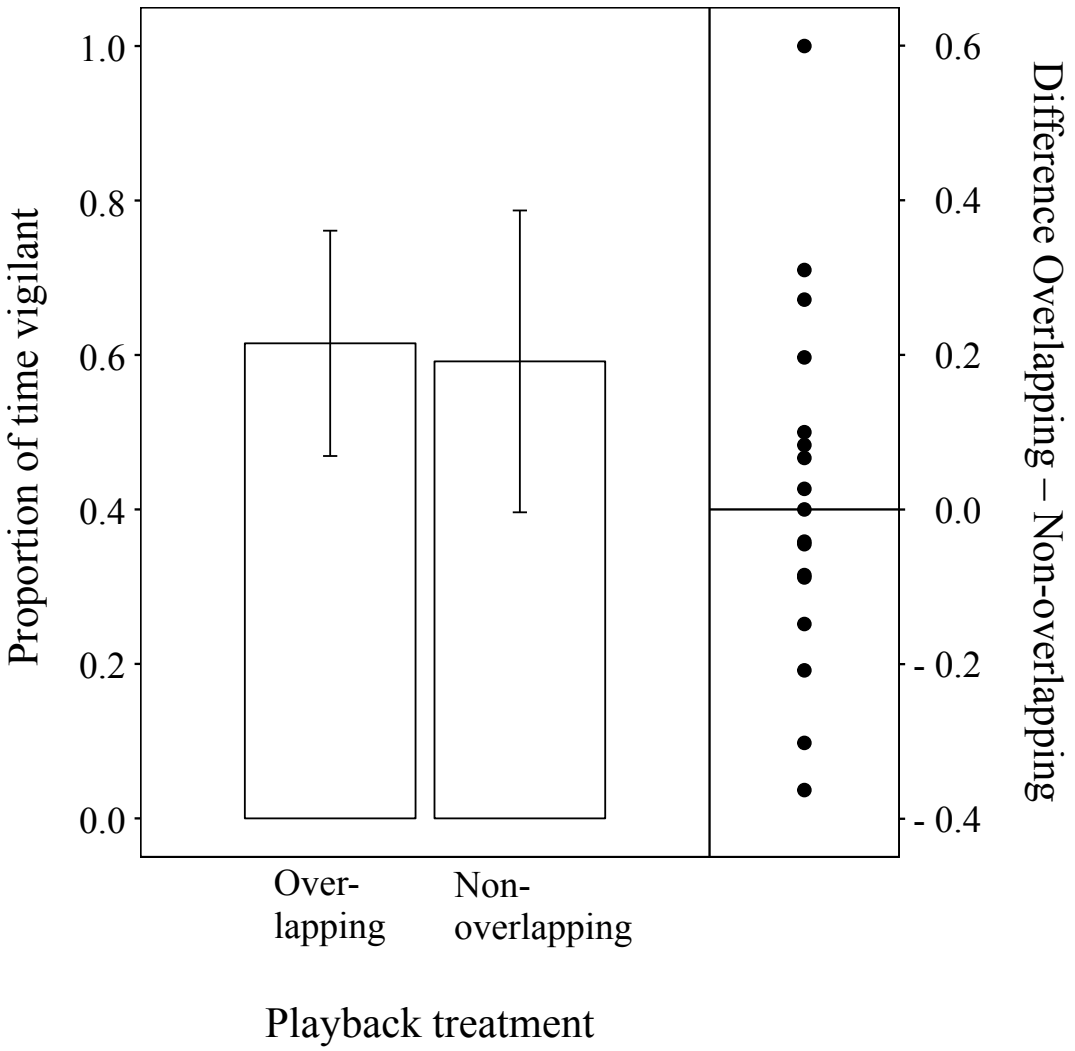
725 **Figure 4**. Proportion of time fairy-wrens spent vigilant (head up) during the 10 s of noise
726 before alarm calls in playback treatments mixed with Overlapping or Non-overlapping noise.
727 Columns show observed means ± SD, and the scatterplot shows the difference in proportion
728 of time vigilant during Overlapping minus Non-overlapping noise at each location. N = 16

729 locations for both treatments; 30/32 recordings had a full 10 s sample, while the video was
730 accidentally cut short in two cases (8.3 and 9.4 s) but adjusted for the shorter duration.
731


(a)
amplitude
12
frequency (kHz)
6
0
200 ms
(b)
amplitude
12
frequency (kHz)
6
0
(c)
amplitude
12
frequency (kHz)
6
0
0
5
10
15
20
time (s)


1.0
0.8
0.6
0.4
0.2
0.0
Proportion fleeing to cover
p = 0.13
p = 0.23
p = 0.03
p = 1.0
Noise 52 dB
Noise 61 dB
Alarm 52 dB
+ Noise 52 dB
+ Noise 55 dB
+ Noise 58 dB
+ Noise 61 dB
Playback treatment


p = 0.004
1.0
0.8
0.6
0.4
0.2
0.0
Proportion fleeing to cover
Over-lapping noise
Non-overlapping noise
Alarm call
+ Over-lapping noise
+ Non-overlapping noise
Playback treatment


Proportion of time vigilant
1.0
0.8
0.6
0.4
0.2
0.0
0.6
0.4
0.2
0.0
- 0.2
- 0.4
Difference Overlapping – Non-overlapping
Over-
lapping
Non-
overlapping
Playback treatment

Why does noise reduce response to alarm calls? Experimental assessment of masking, distraction and greater vigilance in wild birds

You Zhou, Andrew N. Radford & Robert D. Magrath

Supporting Information

Field playbacks

The playback experiments followed our standard protocol for testing responses to aerial alarm calls (Magrath *et al.* 2007, 2009, 2015; Murray & Magrath 2015), using our mobile playback equipment consisting of a Roland Edirol R-05 HR digital recorder, connected to a custom amplifier and a Peerless 810921 tweeter speaker (frequency response 2–11 kHz). We followed a focal individual from about 10 m, and observed it for at least 5 min of undisturbed foraging before playback. Playbacks were carried out when there were no heterospecifics nearby, and the focal bird was about 10 m from the observer and 0.5–10 m from cover. Conspecifics were sometimes nearby, but the focal bird was always the closest bird meeting the playback criteria. We ensured there was no obstruction between the speaker and the focal bird that could affect transmission or obscure our view of the bird's response. We stopped the playback if the bird was disrupted by natural alarm calls or predators (13/192 playbacks in total), and the whole playback was repeated after at least 5 min.

Effect of natural background noise during playbacks

Natural ambient sound was too low to have any substantial effect on the outcome of playbacks. Playbacks to wild individuals were carried out in relatively quiet periods when there was no prominent ambient sound, such as from aircraft or nearby vehicles, or during periods of rain and wind. Then, after each playback, the ambient sound was audio-recorded for 30 s, using the same equipment that was used to record the background noise for playbacks. Amplitudes were then measured in Raven 1.5 Pro and calibrated against a tone of known amplitude. The contribution of ambient sound to the total amplitude experienced by

the focal bird was subsequently calculated using logarithmic rules (Brumm & Zol1inger 2011):

$$\text{Total amplitude } (signal + ambient) \text{ dB SPL} = 10\log_{10}(10^{\left(\frac{L_{signal}}{10}\right)} + 10^{\left(\frac{L_{ambient}}{10}\right)})$$

where L_{signal} is the amplitude of background noise playback and $L_{ambient}$ is the amplitude of ambient sound. In Experiment 1, ambient sound over all recorded frequencies (0–22 kHz) had a mean amplitude of 34.3 dB with a range of 25.5–44. Considering individual playbacks, the maximum increase in amplitude of a background noise playback due to ambient sound was estimated to be 0.36 dB, in a 52 dB playback with 41.4 dB background. In Experiment 2, the mean ambient sound was 38 dB, with a range 31.8–45.4, and so a maximum increase above planned playback levels due to ambient noise was 0.86 dB. These calculations suggest that ambient sound would have little or no effect on bird behaviour compared to the experimental broadcasts. Furthermore, any effect of ambient sound is likely to make it harder to detect experimental effects, and so makes tests conservative.

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